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Spatio-temporal organization of the oribatid mite community in a littoral turf of the Kerguelen Archipelago

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With one figure

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1. Introduction

Up to present time there are few studies concerning the quantitative ecology of soil microarthropod populations, particularly the oribatid mites, in either the Antarctic (TILBROOK 1967; GODDARD 1979; BLOCK 1982; USHER & BOOTH 1986) or the sub-Antarctic ecosystems (WEST 1982, 1984). These ecosystems are particularly interesting because of their simplicity. This simplicity is advantageous since it may give a better understanding of the organization of the community (USHER *et al.* 1979).

In the sub-Antarctic, the coastal ecosystems are the most productive, due to the input of organic matter and nutrients from the sea (SIEGFRIED 1982; BLANKLEY & GRINDLEY 1985; HUREAU 1985; TRÉHEN *et al.* 1985).

Quantitative studies in ad-littoral zone are particularly appropriate since BELLIDO (1982) demonstrated the importance of oribatid mites in these communities that have a homogeneous vegetation structure and a simple microarthropod community.

For this reason an ecological study on oribatid mite community was carried out during two years in a halophilous turf of *Crassula moschata* D. C. in Kerguelen archipelago. The first part of this study concerns the fluctuations in numbers and relations with abiotic factors (BELLIDO & CANCELA DA FONSECA, in press). The present paper deals with the coexistence and distribution pattern of the oribatid mite species.

2. Materials and methods

2.0. Note

The study area is described by BELLIDO & CANCELA DA FONSECA (in press). It is a turf of *Crassula moschata* in which there are two zones; an upper one which is well drained and a lower one which is wetter and more exposed to sea spray.

2.1. Field study

The oribatid mite community was sampled monthly in both zones during fourteen months from February 1978 to March 1979. On each occasion twenty soil cores per zone, each 3.5 cm diameter and 4 cm deep, were taken, and the fauna were extracted in a modified air-conditioned Macfadyen extractor. At the same time the samples were taken, environmental factors were measured. Soil porosity and soil moisture content, in particular, varied between the two zones (BELLIDO & CANCELA DA FONSECA, in press).

2.2. Statistical study

To study the spatial distribution pattern of the two main species present — *Antarcticola* sp. cf. *georgiae* WALLWORK and *Oppia crozetensis* RICHARDS — we chose, to analyse their aggregation

behaviour using Taylor's power law (TAYLOR 1961), one of the many methods existing (CANCELA DA FONSECA & STAMOU 1982), as it gives a satisfactory account of the spatial distribution pattern of a large number of species (TAYLOR, WOJWOD & PERRY 1978). The parameter b of the power law: $s^2 = ax^b$ or $\log s^2 = \log a + b \log x$ (s^2 being the variance, x being the arithmetic mean, and a and b being parameters of the population), is an index which increases with aggregation. This parameter has been applied to different sub-populations (adults and immatures), of the upper and lower zones (2 zones $\times$ 14 months = 28 series of 20 soil cores), but no significant difference was observed between them; therefore, a common index value has been used to characterize each sub-population during the 14 months period 1978–1979.

A second measure of aggregation, where the variance is also a direct function of the arithmetic mean, the Lexis' index, $\lambda^2 = s^2/\bar{x}$ was applied in order to compare it with the preceding one. The Lexis' index is frequently used (ELLIOT 1971; CHESSEL 1978) and particularly for soil microarthropods (CANCELA DA FONSECA 1966, CANCELA DA FONSECA & STAMOU 1982). In the Taylor's law, the aggregation behaviour of the species during the whole period of observation is represented by b , i.e. by a unique value, obtained by regression analysis of the monthly values of the mean and the variance; so to measure the tendency of aggregation of the species over the same period by the Lexis' index, a global index was calculated as the arithmetic mean of its monthly values.

3. Results

3.1. The mites

The community of oribatid mites included only three species, two of which were dominant and occurred throughout the year — *A. georgiae* (Podacaridae) and *O. crozetensis* (Oppiidae). These two species are the most abundant in the general oribatid mite community of Kerguelen Archipelago, representing 14% and 17% respectively (TRAVÉ 1976). The third species, *Liochthonius* sp. cf. *mollis* HAMMER (Brachychthoniidae), was only periodically found in the samples. The immature stages of *A. georgiae* were found throughout the year, whereas those of *O. crozetensis* were only found during the period from the end of the autumn to the start of the winter.

The two zones of the *Crassula* community are dominated by different species of mites. The upper zone is characterised by *O. crozetensis*, since this species accounts for 73% of all individuals. The lower zone is characterised by *A. georgiae* with 99% of individuals. *L. mollis* is present only in the upper zone, with 2% of individuals.

Though the three species can coexist in the same sample units, their adult and developmental stage dimensions are quite different (table 1), which can explain, to a certain extent, their coexistence. The larger species is *A. georgiae* whose length is on average 2.2 times the length of *O. crozetensis*. Furthermore, the mean length of *O. crozetensis* is about 1.6 times that of *L. mollis*, the smaller species. Concerning *A. georgiae*, the increase in size (length) from one developmental stage to another is between 1.19 and 1.32 (hence very close). There is no overlap in the size ranges of the different developmental stages.

Table 1. Size comparisons between species and age classes

	length (μm)			length ratios	
	minimum	mean	maximum		
<i>Antarcticola</i> (A)					
Adults (AA)	649.30	683.00	739.55	AA/A3 = 1.19	AA/OA = 2.20
Tritonymphs (A3)	513.40	573.80	604.00	A3/A2 = 1.28	
Deutonymphs (A2)	407.70	442.10	483.20	A2/A1 = 1.32	
Protonymphs (A1)	282.00	334.00	378.00	A1/AL = 1.30	
Larvae (AL)	234.00	255.60	270.00		
<i>Oppia</i> (O)					
Adults (OA)	294.00	309.80	324.00		OA/LA = 1.64
<i>Liochthonius</i> (L)					
Adults (LA)	177.60	187.80	196.10		

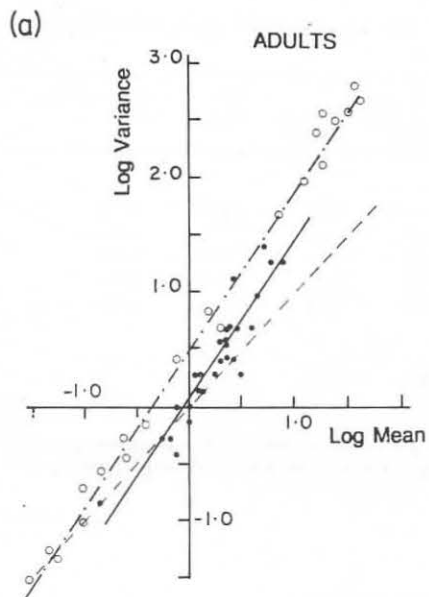


Fig. 1. The relationship between log (variance) and log (mean): (a) for *Oppia* (○) and *Antarcticola* (●) adults, and (b) for the different developmental stages of *Antarcticola* (●). The dashed line (-----) has $b = 1$ and $\log a = 0$; observed regression line are *Antarcticola* (—) and *Oppia* (— · —). See Table 2 for the regression coefficients.

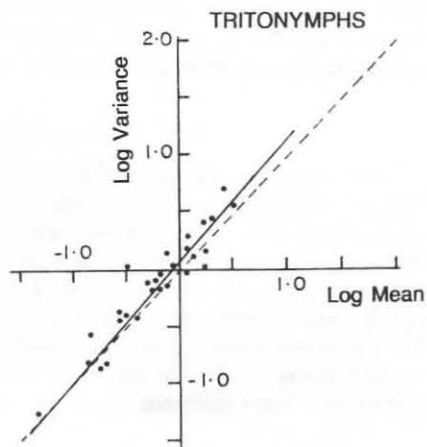
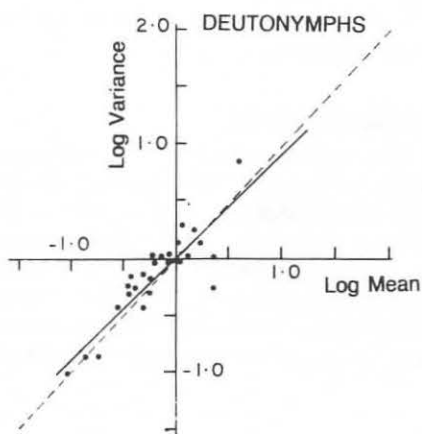
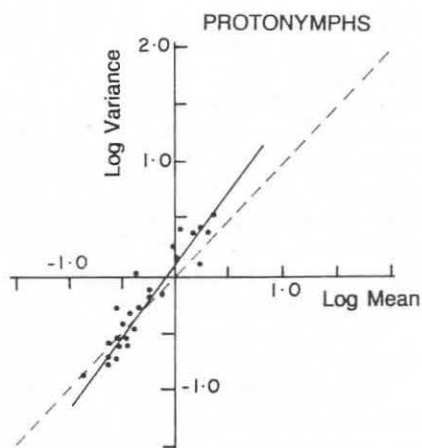
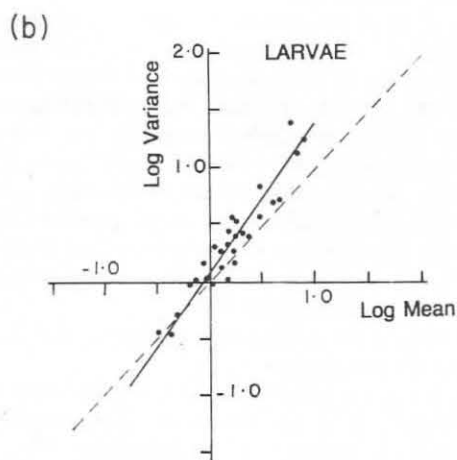


Table 2. A comparison of TAYLOR aggregation index and the variance/mean ratio, calculated from both upper and lower zones

Group	Months	DF	Intercept (log a)	Slope (b)	C. I. Slope		R ² (%)	$\lambda^2 = s^2/\bar{x}$
					Lower	Upper		
Antarteticola								
Adults	28	26	0.06	1.39	1.20	1.59	89.40	1.64
Larvae	28	26	0.07	1.28	1.11	1.45	90.00	1.47
Protonymphs	28	26	0.11	1.27	1.09	1.45	89.10	1.20
Deutonymphs	28	26	0.00	0.90	0.71	1.08	79.40	1.11
Tritonymphs	28	26	0.08	1.03	0.91	1.15	92.10	1.25
Oppia								
Adults	20	18	0.49	1.40	1.34	1.46	99.20	6.54
Juveniles	8	6	0.24	1.39	0.93	1.86	89.90	2.23

Note: a, b and λ^2 are defined in section 2.2.; the confidence interval (95 %) of b is given, and R², the coefficient of determination, represents the percentage of the total variation explained by the regression.

3.2. The spatial distribution pattern

As it would be expected, the Taylor's and 'Lexis' indices did not give the same results (table 2), Lexis' index being more sensitive to the values of the variance. Thus, for the same values of the arithmetic mean, the variance is higher for *O. crozetensis* than for *A. georgiae* (fig. 1a) and therefore the mean value of λ^2 for the adults of the first species is almost four times larger than for the second one, whereas b for the two sets of adults is almost the same (table 2). However, the different species and age classes are ranked nearly in the same order according to the two indices, for which Spearman's rank correlation coefficient is 0.9 (significant at $\alpha = 0.05$). For the adults (fig 1a) the maximum values of the variances of *O. crozetensis* are greater than the maximum values of the variances of *A. georgiae* for the same values of the mean. However, the slopes of the two lines are virtually identical. Comparison of the adults and juveniles of *A. georgiae* in fig. 1 indicates that values of the Lexis index are affected both by the slope and intercept of these regression lines.

Finally one can hypothesize that the index b measures the aggregation tendency whereas the Lexis index is also related to the largest values of the variance.

It is therefore concluded that the adults of both species, although their population densities are different, show the same tendency to aggregate. However, the adults of *A. georgiae* are significantly more aggregated than the juveniles. Inspection of the data shows three groups, according to the values of b (table 2; fig. 1): the adults ($b = 1.39$), more aggregated than the larvae and protonymphs ($b = 1.28$ and 1.27 respectively), and tritonymphs and deutonymphs ($b = 1.04$ and 0.90 respectively) randomly distributed. The reason for the tritonymphs and deutonymphs being non-aggregated is unknown.

3.3. Intraspecific and interspecific coexistence

Although the aggregation indices give different information on each of the sub-populations' distribution, it is possible from the same data to measure the degree of relative occupation of the available soil space for the different sub-populations. In order to do this, SCHOENER's (1968) niche overlap index has been used since it seems to be the most accurate over the range of values from 0.07 to 0.85 (LINTON, DAVIES & WRONA 1981). It is based on the spatial distribution principle, i.e. on the degree of occupation of different resources by the same species. Thus, it measures the percent overlap of two species distributions.

According to the nature of coexistence to measure — spatial or temporal — the index parameters have different significations.

Therefore

$$R_{ij} = 1 - 1/2 \sum_{k=1}^n |p_{ik} - p_{jk}|$$

where p_{ik}, p_{jk}	are the probability of the k th resource being used by the i th and j th species; hence in practice $p_{ik} = n_{ik}/N_i$ and $p_{jk} = n_{jk}/N_j$	
and p_{ik}, p_{jk}	spatial coexistence the number of individuals of species i and of species j in the sample unit k	temporal coexistence the number of individuals of species i and of species j in the sample at the period k
N_i, N_j	the total number of individuals of species i and species j in the whole sample	the total number of individuals of species i and species j for the n time periods
n	the number of sample units	the number of time periods

Although the index for spatial coexistence is rarely used in the study of the soil fauna, it has been applied to other arthropod communities, for example in a study of the spatio-temporal coexistence in a spider community (UETZ 1977).

Table 3 gives the results for comparing the adults of *A. georgiae* with the adults of *O. crozetensis* and with two of the juvenile stages of *A. georgiae*. For the spatial coexistence all of the indices have a value of nearly 0.5. This relatively small value indicates that the distribution of the individuals in the sample units is different from the distribution of the different sub-populations under study. For temporal coexistence, there is a small overlap between the adults of *A. georgiae* and *O. crozetensis* (0.44), whilst the intraspecific coexistences are all much larger. The product of the two coexistence indices (assuming the independence of the two resources), or the "overall overlap" (PIANKA 1975), takes into account both the spatial and temporal aspects of coexistence. The values obtained show that coexistence is clearly smaller at the interspecific level (0.21) than at the intraspecific level (about 0.4 on both the upper and lower *Crassula* zones).

Table 3. The spatial and temporal coexistence, between and within species, as measured by SCHÖENER's overlap index

Crassula Zone	Antarcticola Adults vs				
	Oppia Adults	Antarcticola Tritonymphs		Antarcticola Larvae	
	Upper	Upper	Lower	Upper	Lower
Spatial coexistence-R(S)	0.48	0.54	0.50	0.52	0.60
Temporal coexistence-R(T)	0.44	0.79	0.70	0.81	0.68
R(S)* R(T)	0.21	0.43	0.35	0.42	0.41

Note: Only three pairwise comparisons (*Antarcticola* adults vs others) are given here.

4. Discussion

The spatial distribution of the soil fauna is usually aggregated. The different studies on this subject generally concern measuring the degree of aggregation (BERTHET & GÉRARD 1965) or the causes of aggregates. Taylor's power law model has proved to be appropriate for measuring aggregation; TAYLOR, WOIWOD & PERRY (1978) gave examples of oribatid mite data from the literature, with index values varying between 1.00 and 1.74. In their data for the Oppiidae, the values varied between 1.29 and 1.42 which are close to the values calculated for *O. crozetensis* (1.40) here. USHER (1975) pointed out that the oribatid mites generally showed larger b values (i.e. more aggregated) than mesostigmatid mites, probably in relation to their feeding behaviour.

There are several causes of aggregation. Among the different categories described by HUTCHINSON (1953), the most frequently demonstrated for soil microarthropods (USHER 1976) are the social (intraspecific interactions), reproductive (distribution linked to the egg laying pattern) and vectorial (distribution related to the abiotic environment) types. For example, the Antarctic prostigmatid mite, *Nanorchestes berryi*, has two spatial patterns, the smallest being reproductive in the juvenile stages and social in the adult stage, and the largest being vectorial (USHER & BOOTH 1986).

The data from the Kerguelen Islands are probably similar. The change in the aggregation index during development of *A. georgiae* seems to indicate that the adults could be actively aggregated, the larvae and protonymphs passively aggregated in relation to the site where the eggs were laid, and the deutonymph and tritonymph stages actively dispersing and hence appearing randomly distributed. However, in our research only the aggregation at the smallest level could be measured due to the random sampling pattern. The vectorial type of aggregation could not be investigated with such a set of soil cores. This may be why there was no significant relationship between the moisture content of the cores and the numbers of each species in those cores, as was stated by BELLIDO & CANCELA DA FONSECA (in press).

However, within the *Crassula* ecosystem, it was observed that *O. crozetensis* prefers less salty and better drained environments than *A. georgiae* [BELLIDO & CANCELA DA FONSECA, in press]. The two species coexist only on the upper zone farthest from the sea, since *O. crozetensis* is almost absent from the zone more directly exposed to salt spray. At the spatio-temporal level the coexistence is rather small (Table 3) which indicates a clear separation between the ecological niches of the two commonest species on the site. This may be due to the difference in size of the two species (table 1), but it could also be related to their trophic behaviours, as it has been suggested for other oribatid mite species (CANCELA DA FONSECA, in press). There are few studies of niche separation in soil microarthropods in the literature. ANDERSON (1978), in a study of forest soil oribatids, has suggested that there are competitive interactions between species, both at the trophic level and at the level of colonization of microhabitats. The great diversity of forest soil oribatid communities contrasts strongly with the species poorness of the *Crassula* ecosystem. However, one must also take into account the available microhabitat diversity (ANDERSON 1978). In comparison with the forest, the *Crassula* ecosystem looks poor in microhabitats on account of the homogeneity of plant cover and the small depth of the soil.

In relation to the coexistence between the developmental stages of *A. georgiae*, the spatio-temporal coexistence (table 3) looks rather small and would be an indication of the way that adults and immature stages exploit the available microhabitats independently of each other. Such an interpretation is similar to the results of BELLIDO (1979) on *Carabodes willmanni* BERNINI: both the adults and immature stages of that species eat vegetable (lichen) matter but at different decomposition stages (and their vertical microdistribution is also different).

5. Conclusion

The study of the spatial distribution of the two dominant species, *O. crozetensis* and *A. georgiae*, shows that they have a similar aggregation behaviour, at least when adults. The main difference between the two species is their population density, and hence the number of individuals that form an aggregation. There is evidence of spatial separation of the species at two levels. First, at the ecosystem level, there seems to be separation related to the environmental conditions, probably related to the salinity of the soil. Second, at a smaller level (the size of the core used for sampling), the separation is likely to be related to the heterogeneity of the available resources of the microhabitats. For *A. georgiae*, the spatial distribution pattern and the microhabitat choice seem to be determined, at least partially, by the developmental stage of the species. In order to verify these hypotheses, one requires ecophysiological studies, investigating precisely the adaptations of each stage to the water and salinity content of the soil, and more detailed environmental studies, allowing the exploitation of microhabitats by the two species to be quantified.

6. Acknowledgements

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Synopsis: Original scientific paper

BELLIDO, A., & J. P. CANCELA DA FONSECA, 1988. Spatio-temporal organization of the Oribatid mite community in a littoral turf of the Kerguelen Archipelago. *Pedobiologia* **31**, 239—246.

In 1978—1979 a quantitative study of oribatid mite community was undertaken on a littoral halophilous *Crassula moschata* D. C. turf, on a monthly sampling basis. Two facies related to the soil moisture content are compared: a dry facies (upper zone) and a wet facies exposed to sprays (lower zone).

The community structure is very simple with two main species: *Antarcticicola* sp. cf. *georgiae* dominant in the lower zone, and *O. crozetensis* Richters dominant in the upper zone. A rarer third species was present only in the upper zone: *Liochthonius* sp. cf. *mollis* HAMMER.

O. crozetensis population, with numbers much higher, shows the same spatial pattern than *A. georgiae*. But the spatial pattern changes during the development of *A. georgiae*.

Beyond the body size, the two species exploit differently the available space, being scarcely present together in the same space-unit all through the year.

Nevertheless, a higher synchronism adults-immatures in the exploitation of the spatial resource was observed in the *A. georgiae* populations.

The spatial distribution pattern observed is, on one hand probably related to the soil salinity, and on the other hand probably in relation with the heterogeneity of the available resources at microhabitat level.

Key words: Acari, Oribatida, *Antarcticicola georgiae*, *Oppia crozetensis*, Subantarctic, littoral turf, spatial pattern, spatio-temporal overlap.